Fig. 4. Lateral view of the pterygoid of *Tetrapteryx paradisea*. The hemipterygoid and palatine bear the same relation to the main body of the pterygoid as in *Oceanodroma* (fig. 2).

Fig. 4 *a*. In this figure, which represents the external lateral view of fig. 4, the hemipterygoid element is seen to be more degenerate than in *Pygoscelis* (fig. 3 *a*), and the vomer is in consequence supported entirely by the palatines.

Fig. 5. Lateral view of the pterygoid of a nestling of *Steatornis caripensis*, wherein the hemipterygoid element has not yet segmented off from the main shaft.

Fig. 5 *a*. The lateral view of the pterygoid of an adult *Steatornis caripensis*. The distal end of the pterygoid has now segmented off to form the hemipterygoid. It is connected with the main shaft by a sigmoid articulation, but remains traceable throughout life by reason of the fact that its distal end projects above the palatine.

Fig. 5 *b*. Ventral aspect of fig. 5 *a*, showing the transverse articulation with the palatine and fused hemipterygoid element.

Fig. 6. Lateral view of the pterygoid of the Rook (*Corvus frugilegus*). The hemipterygoid just reaches the vomer. Later, on its fusion with the palatine, the articulation with the main body of the pterygoid is *oblique*, not transverse as in the majority of Neognathæ.

Fig. 7. Lateral view of the pterygoid of *Megalæma marshallorum*. Compared with fig. 6 it will be seen that in *Megalæma* the pterygoid has reverted to the original, Palæognathine, unsegmented condition, the hemipterygoid being continuous with the main shaft and extending forward to support the vomer, which is entirely free from the palatine.

Fig. 8. Lateral view of the pterygoid of *Bucco Dysoni*. The pterygoid, as in fig. 7, is unsegmented. The vomer is vestigial or wanting. By further specialization the palatine has almost completely fused with the pterygoid, only a slight cleft marking the distinction between the two.

Fig. 8 *a*. Ventral view of fig. 8, showing the last traces of an originally transverse palato-pterygoid articulation.

Explanation of Letters.

h.pt.=hemipterygoid.
inf.t.foss.=inferior temporal fossa (quadrato-jugal fossa).
mx.p.=maxillo-palatine process.
pa.=palatine.
par.=parasphenoidal rostrum.
p.p mx.=palatine process of premaxillary.
pt.=pterygoid.
vo.=vomer.

On the Corallum of *Turbinaria*. By S. Pace, F.Z.S. (Communicated by H. M. Bernard, M.A., F.L.S.)

[Read 18th April, 1901.]

The Formation of the Cup.

No actual observations upon the early stages in the growth of the remarkable cup-shaped corallum of *Turbinaria* appear to have been yet recorded. It has usually been assumed that the parent polyp becomes submerged in the common cœnenchyma of the coral, and that its calicle is not recognizable after the corallum has attained the cup form. Thus Mr. H. M. Bernard, an admitted authority on this group, writes *:—"A ring of buds shoots up round and from the sides of the parent polyp, together forming a cup, the wall of each bud rising up as a distinct cone above the level of the fusion of their walls to form the common cœnenchyma. The parent polyp dies away, and its primitive protuberant cone is immersed under the cœnenchyma formed from the fusion of the walls of a ring of daughters. These daughters carry on the colony, the budding of the daughters being limited to their free or outer sides, *i. e.* to the sides turned away from the axis of the cup." To illustrate his comparison with what occurs in the case of *Madrepora*, Mr. Bernard gives the two diagrams† which are copied in figs. 1 & 2. The supposed dying away of the parent polyp in *Turbinaria* was evidently assumed in order to explain the fact that it is so very unusual to find any trace of a calicle occupying a central position at the base of the cup.

An examination of younger growth-stages‡ than are contained in the British Museum collection, and the dissection of several small cups, have revealed the interesting fact that the parent polyp does not die away, but that it bends over to one side and takes part with its daughters in forming the rim of the cup. In a normal cup the parent calicle can always be traced as one, generally the largest, of the innermost ring of calicles.

* Ann. Nat. Hist., ser. 6, vol. xx. (1897), pp. 131–2.

† Catal. Madrep. Corals Brit. Mus., vol. ii. London, 1896.

‡ The corals collected by me in Torres Straits I have presented to the British Museum.

The actual process is represented diagrammatically in figs. 3 to 10; and fig. 5 may be taken instead of Mr. Bernard's diagram

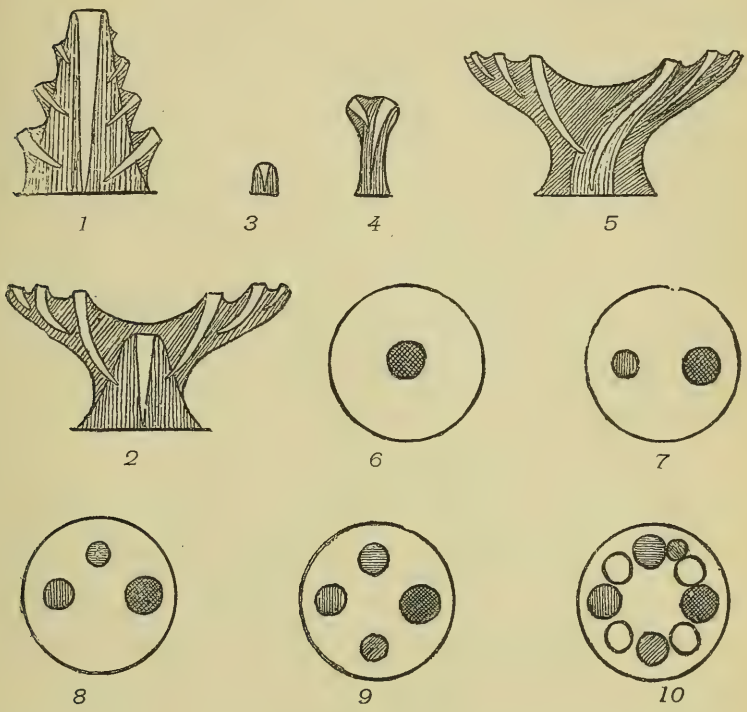


Fig. 1. Diagram of *Madrepora* showing the relationship of the parent calicle to the corallum, after Bernard.

Fig. 2. Erroneous diagram of *Turbinaria*, after Bernard.

Figs. 3–5. Diagrams illustrating the formation of a Turbinarian colony and the fate of the parent calicle.

[Figs. 1–5 are similarly shaded.]

Figs. 6–10. Diagrams of successive transverse sections of the stem of a young corallum to illustrate the mode of budding. The calicles are similarly shaded in each diagram.

(fig. 2) for comparison with that of *Madrepora* (fig. 1). It will be seen that the agreement between the two types is even closer than was suggested by Mr. Bernard; the only difference being that while in *Madrepora* the parent polyp retains its axial

position and grows up in advance of its daughters, so that it is at all stages the terminal polyp of the colony, in *Turbinaria* the parent polyp bends away from its first daughter-bud and then grows up together with and alongside its daughters, so that eventually it comes to form one of a ring of calicles of which its daughters are the other members.

While the central area of the cup is typically wholly cœnenchymatous, occasional examples are met with in which a calicle does occupy a central position within it; but, as already stated, this is a very unusual occurrence, and it would appear to be the result of a secondary torsion on the part of either the parent or of one of the daughter polyps. I have also noticed in a few specimens the existence of a slight central elevation which rather suggested that a calicle was buried at that point; but as no dissection was made, it may well be that the appearances observed were in reality due to the presence of some commensal or parasite.

The Variation of the Corallum.

A few words regarding some of the modifications which the Turbinarian cup undergoes with advancing age, and by the direct influence of its environment, may not be out of place, since I have had rather exceptional opportunities* for the observation of corals and their habits, and since the so-called species of *Turbinaria* have been to so large an extent founded upon what are in reality but acquired characters. Bernard, in his Catalogue of the British Museum *Turbinariæ*, found himself obliged to group them according to the forms ultimately assumed by the cup; but, inasmuch as it was obvious that many of these might be adaptational or even accidental, he pointed out that his classification was purely morphological, and only to be regarded as a provisional one. It will now be my endeavour to show that the variations of a Turbinarian colony from the primitive cup-shape—the "crateriform" type of Bernard—*can* be readily explained by reference to the conditions under which the coral has

* During a stay of nearly three years in Torres Straits, while engaged in the investigation of the commercial pearl-shell, some thousands of examples of *Turbinaria* in all growth-stages have passed through my hands or under my notice. Turbinarians are exceedingly plentiful on the reefs in this region, and young individuals, as well as large cups, are very commonly found on the backs of the pearl-shell collected by divers.

grown; though it by no means follows that heredity plays no part in determining the form of growth assumed by the corallum under any particular conditions, and it may well be that the *tendency* towards one type rather than another is inherited; this, however, can only be established by experiment.

As might be expected, the largest and most perfect cups are those formed at depths below the tidal zone, in clear water, and where the growth of the corallum is unrestricted by neighbouring objects*.

Above extreme low-water mark there is a greater tendency for the coral to lose its cup-shape, and to become irregular by the folding and crumpling of its walls and by the adoption of an encrusting habit. Again, specimens are common on the reefs in which certain calicles have budded to form secondary, more or less independent, colonies: subsidiary cups† may thus be formed within the parent cup, and some such individuals present a regularly "storied" appearance. In other cases the secondary colonies, instead of forming cups, take on an arborescent growth like that of a *Madrepora*. This modification‡, which I may term the "madreporiform" type, is a not uncommon one where the coral is growing at the bottom of a hole in the reef, and where growth in a vertical direction is of obvious advantage to the colony.

When a *Turbinaria* grows upon a shelf or ledge of rock it generally loses its cup-form; the side turned away from the free edge of the shelf ceases to grow, and the corallum thus becomes a more or less flattened, expanded plate§ overhanging the ledge.

When, during growth, the lower surface of the cup comes into contact with the substratum, irregular root-like outgrowths will

* At the time of publication of the British Museum Catalogue the largest cup in that collection was stated (with a certain amount of pride) to measure as much as sixteen inches in diameter; such a specimen is, however, in reality quite a small one compared with the giants occurring on the shelling grounds in Torres Straits.

† These daughter cups, the result of proliferation of individual polyps, must not be confounded with the cup-shaped folds of the wall of the parent cup, which are of much more common occurrence.

‡ A very good example of this type of growth is figured by Ortmann as *T. maxima*—Zool. Jahrb., Syst. vol. iii. pl. vi. fig. 4.

§ The specimens of *T. reniformis* and *T. foliosa* figured by Bernard (Catalogue, pls. xvii. & xviii.) probably owe their form to this cause.

generally arise at the points of contact; and the specimen may thus acquire an appearance rather suggesting that of the Banyan tree with its numerous false stems. This type of growth has been described as *T. radicalis* by Bernard*.

Not infrequently a cup becoming accidentally broken from its stalk continues to live in this detached condition; and, if it has at the same time been inverted, subsidiary cups will often be formed upon its upturned lower surface.

In addition to these modifications, due mainly to position, there are others which direct observation on the reef has enabled me to trace to another cause: namely, the danger of becoming silted up or clogged with the fine mud which is always a prominent feature on a coral-reef. This is apparently the greatest evil which a coral has to dread, and the structure of the corallum is frequently much modified in such a manner as to adapt it to life on muddy ground. Under such conditions the cup of a *Turbinaria* is often flattened out, the "peltate" type of Bernard, and the colony may even assume a convex form; or else the cup may be cleft on one side, or perforated at its base, so as to render it impossible for any silt to lodge within it.

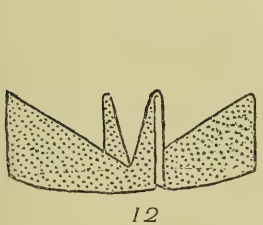
Where the side of the original cup becomes cleft, one of the lobes thereby formed may extend round the outside of the cup, and, the growth of the other lobe being arrested, the corallum may take on a roughly spiral form, and silting will be obviated by the presence at the base of the corallum of a continuous gutter by which any foreign matter will be carried off. Those forms which Bernard has termed the "*Turbinariæ frondentes*" belong to this type of growth†. A very common method by which a Turbinarian defends itself against silt is that in which at an early stage the margin of the cup, or rather disc, becomes bent down at regular intervals or frilled‡, so that with further growth, the details of which are susceptible of various modifications, a very perfect gutter system results. In what

* Brit. Mus. Catalogue, pl. ix.

† The specimens of *T. auricularis* and *T. calicularis* figured by Mr. Bernard (Brit. Mus. Catal., pls. x. & xi.) are poor examples of this type. It is shown in its most perfect form by a specimen of *Montipora* (in which genus this modification is much more common than in *Turbinaria*) figured by Mr. Saville Kent in his 'Naturalist in Australia,' pl. xxiv. p. 146.

‡ The specimen of *T. peltata* figured by Mr. Bernard (Brit. Mus. Catal., pl. vi.) shows this very well.

Mr. Bernard has termed the "bifrontal" type of growth, the elevated folds become greatly extended and their apposed lower surfaces fuse together all over: a corallum may thus arise which consists of numerous close-set vertical plates bearing polyps upon each of their faces and connected with each other by but a slight attachment at their bases. The narrow, more or less radial, interspaces of this type are practically open all round and so afford no lodgement for silt*. In Bernard's "foliate" and "mesenteriform" types the elevated folds, instead of fusing together back to back, persist either as open frills, or, meeting, fuse only along the lines of junction. In this way a corallum consisting of a series of connected cylinders or cups, open at their bases, and bearing polyps alternately upon their inner and outer faces, may arise. By the suppression of the elevated folds a series of cups, each having, like the parent cup, an internal polyp-bearing surface, may be formed; while an exceedingly interesting extension of this type of growth is afforded by those cases in which the growth of the depressed folds has been arrested, so that the corallum has come to consist of a series of



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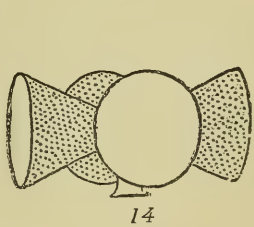

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Figs. 11–14. Diagrams to show the origin of various types of growth by the folding of the margin of the primitive cup or disc. The polyp-bearing surfaces are dotted.

* A series of specimens well illustrating this type is figured by Mr. Bernard as *T. gracilis*, Brit. Mus. Catal., pl. xxiii.